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Mechanisms of arrested succession in shrublands: root and shoot competition between shrubs and tree seedlings

F.E. Putz[a] and C.D. Canham[b]

[a]*Department of Botany, University of Florida, Gainesville, FL 32611-2009, USA*
[b]*Institute of Ecosystem Studies, The New York Botanical Garden, Box AB, Millbrook, NY 12545, USA*

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ABSTRACT

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Relative effects of above-ground and below-ground competition from shrubs (*Cornus racemosa* and *Rhus glabra*) on the growth of tree seedlings (*Acer rubrum* and *Fraxinus americana*) were assessed with a field experiment in the Hudson Valley, New York. Shade on tree seedlings planted in clumps of shrubs was reduced by guy-wiring back overtopping shrub crowns. Root competition was reduced by cutting a 0.5 m deep slit around the seedlings and inserting root restriction cloth. We also applied a combined treatment to some seedlings and reserved others as controls. In the field with the most severely drained and nutrient-poor soil, reduction of root competition increased relative growth rates of the seedlings while opening the canopy had no effect. Trenching and shade reduction around tree seedlings planted in shrubs clumps in a more mesic old field with a stony silt loam soil increased relative growth rates only if the treatments were combined. In a wet field with alluvial soil, guy-wiring back overtopping shrubs greatly increased seedling growth but trenching alone had no effect. Tree encroachment into shrub-dominated stands can be reduced by both root and shoot competition, but the severity of competition in these arenas varies with site conditions; below-ground competition is intense where soil resources are limited whereas the effects of shade are relatively more severe on sites with good soil.

INTRODUCTION

Dense shrub stands that develop after agricultural land is abandoned often persist for decades before being overtopped by trees. This phenomenon has been described in some detail in the northeastern USA, where encouraging shrubs has potential as an environmentally sound method for reducing tree encroachment in power line rights-of-way (e.g. Pound and Egler, 1953; Niering and Goodwin, 1974; Phillips and Murdy, 1985). In silviculturally managed areas, in contrast, shrubs are often perceived as a major impediment to

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tree growth (e.g. White and Newton, 1989). Although it is clear that the presence of shrubs is often detrimental to the growth of young trees, the nature of the interaction has not been clearly elucidated. It is not even clear that competition is the major mechanism responsible for delays of tree encroachment in shrub-dominated areas; seed dispersal and predation, for example, may limit tree seedling establishment.

We conducted a field experiment designed to determine whether tree seedling growth is suppressed by shrubs and, if there is competition, whether it is more severe above ground or below ground. Our study was motivated in part by the observation that root competition is often more severe than shading effects (for a review see Wilson, 1988). We conducted the experiment in three shrub-dominated fields representing a range of soil moisture and nutrient availabilities to determine the extent to which site conditions influence the nature of shrub–tree interactions.

STUDY SITE

This study was conducted in three abandoned agricultural fields at the Mary Flagler Cary Arboretum, Hudson Valley, New York (41°50′N, 73°45′W) where mean annual precipitation is 1020 mm and July temperatures average 22.4°C (Glitzenstein et al., 1990). The growing season during which this experiment was conducted (1989) was similar to long-term averages in regards to total and monthly rainfall. The most xeric and nutrient-poor site ('Gifford') was used primarily for pasture until abandonment 50–60 years ago. The soil is a well-drained gravelly loam derived from glacial outwash (Secor et al., 1955). The 'Saccomanda' field is on the lower slope of a hill and was used as an orchard and pasture. The soil in this field is a slaty silt–loam with abundant large stones. The 'lowland' (wettest) field has a silty clay loam soil derived from alluvial material and alternately supported intensive agriculture or was cut for hay until about 25 years ago.

METHODS

To determine the effects of above-ground and below-ground competition from shrubs on the growth of tree seedlings, 1-year-old nursery grown *Acer rubrum* (red maple) and *Fraxinus americana* (white ash) seedlings were planted under thickets of *Cornus racemosa* (gray dogwood) and *Rhus glabra* (smooth sumac). These tree species were selected because they are common invaders of shrub-dominated stands over a wide range of sites in New York. Furthermore, both tree species continue to produce leaves throughout the summer, i.e. they have indeterminate growth (Marks, 1975). The shrub species are both common and often form dense monospecific clumps with closed canopies 1.5–2.5 m above the ground.

Treatments were assigned at random to four *A. rubrum* seedlings planted in each of eight *C. racemosa* clumps in each of three abandoned agricultural fields. The treatments were: reduction of root competition, reduction of shoot competition, combined above-ground and below-ground treatments, and a control. Below-ground competition between shrubs and planted tree seedlings was reduced by cutting a deep slit (40–50 cm deep or until large stones interfered) with a sharp blade around each seedling. To prevent root encroachment into the roughly 0.2 m^2 circular area around each seedling, root

TABLE 1

Growth of *A. rubrum* seedlings planted under eight clumps of *C. racemosa* in each of three old fields. The treatments were to guy back overtopping shrubs (Sun), eliminate root competition by cutting roots around the seedlings (Trench), and a combined treatment (Sun–Trench)

	% Canopy open	Relative growth rate (% day^{-1})	
		Height	Basal area
Lowland (rich soil)			
Control	3.7	0.0134	0.34
	(1.10)	(0.066)	(0.133)
Trench	4.0	0.22	0.25
	(0.97)	(0.085)	(0.107)
Sun	81.4	0.75*	0.57
	(4.77)	(0.230)	(0.224)
Sun–Trench	82.3	0.95	0.84
	(4.78)	(0.111)	(0.331)
Saccomanda (intermediate)			
Control	5.2	0.16	0.61
	(0.82)	(0.092)	(0.160)
Trench	3.7	0.52*	1.04*
	(0.31)	(0.140)	(0.232)
Sun	80.5	0.41*	1.28*
	(6.72)	(0.088)	(0.117)
Sun–Trench	78.5	1.08	1.88
	(4.44)	(0.202)	(0.207)
Gifford (poor soil)			
Control	4.8	0.12	0.29
	(1.11)	(0.042)	(0.110)
Trench	6.72	0.68*	0.82*
	(1.90)	(0.134)	(0.217)
Sun	90.8	0.15	0.48
	(0.99)	(0.069)	(0.159)
Sun–Trench	89.4	0.78	1.01
	(1.58)	(0.229)	(0.230)

Within sites, an asterisk next to the mean for the sun or trench treatment indicates a significant effect ($P<0.05$). F-values for all 2×2 factorial ANOVA were significant ($P<0.01$); standard errors are reported in parentheses under the means. There were no significant interactions.

TABLE 2

Growth of *A. rubrum* seedlings in clumps of *R. glabra* and *F. americana* seedlings in *C. racemosa* clumps in the Saccomanda (intermediate site quality) old field

	% Canopy open	Relative growth rate (% day^{-1})	
		Height	Basal area
A. rubrum under *R. glabra*			
Control	5.7	0.04	0.14
	(0.85)	(0.030)	(0.085)
Trench	4.3	0.23*	0.38
	(0.62)	(0.166)	(0.207)
Sun	78.3	0.21*	0.40
	(3.90)	(0.108)	(0.082)
Sun–Trench	76.2	0.79	0.87
	(7.09)	(0.309)	(0.261)
F. americana under *C. racemosa*			
Control	3.8	0.01	0.16
	(0.40)	(0.004)	(0.058)
Trench	3.8	0.04	0.36*
	(0.59)	(0.004)	(0.176)
Sun	86.6	0.01	0.49*
	(3.17)	(0.007)	(0.190)
Sun–Trench	79.2	0.22*	1.01*
	(4.16)	(0.078)	(0.224)

An asterisk next to the mean for the sun or the trench treatment indicates a significant effect ($P<0.05$); an asterisk next to the combined treatment indicates a significant interaction. See Table 1 or the text for explanation of the treatments.

restriction cloth (Never Weed Landscape Fabric, Gilbert and Bennett Co., Georgetown, CN) was inserted into the slits before they were tamped closed. This tight mesh fabric is permeable to water and gases but does not permit root penetration. Shade cast by shrubs was reduced without greatly modifying below-ground conditions by guy-wiring back shrub crowns that overtopped the planted tree seedlings. These treatments were also applied to sets of four *A. rubrum* seedlings planted in six *R. glabra* clumps at one site (Saccomanda) and to sets of four *F. americana* seedlings planted in eight *C. racemosa* clumps in the same area. Canopy cover was estimated with a spherical densiometer (Lemon, 1956) held directly over each seedling. The effects of soil disturbance associated with root cutting on drainage and aeration were mimicked by making the same total length of cuts along eight lines radiating out from the seedlings.

Soon after planting and applying treatments (mid-June), seedling basal diameters and heights were measured. Initial above-ground biomass (oven dry weight, g) was estimated from allometric regressions based on randomly se-

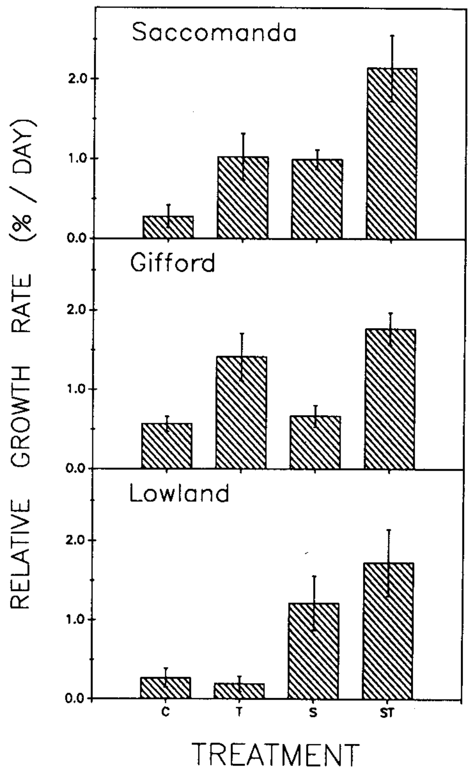

Fig. 1. Relative growth rates of above-ground dry weight of *A. rubrum* seedlings planted in clumps of *C. racemosa* in a wet old field with alluvial soil (lowland), a dry old field with soil derived from glacial outwash (Gifford), and a mesic old field with silt loam soil with large stones (Saccomanda). The treatments were to reduce root competition by trenching around the seedlings (T), increase light by guy-wiring back overtopping shrub crowns (S), the combined treatment (ST), and controls (C). $N=8$ seedlings per treatment in each site (mean $\pm$ 1 SE).

lected samples ($n=11$) from the nursery grown seedlings. Regression equations for *A. rubrum* and *F. americana*, respectively, were as follows:

$$\text{Above-ground Dry Weight (g)} = 0.024\ (BA) + 0.028\ (H),\ R^2 = 0.99$$

$$\text{Above-ground Dry Weight (g)} = 0.039\ (BA) + 0.040\ (H),\ R^2 = 0.97$$

where BA is basal area (mm^2) and H is height (mm).

When the experiment was terminated in late August, basal diameter and height were again measured and the seedlings were clipped at ground level to determine above-ground biomass. The seedlings were dried to a constant weight at 70°C. Relative growth rates were calculated for above-ground dry weight, basal diameter, and height as:

$$\text{RGR} = (\ln (S_2) - \ln (S_1)) / (t_2 - t_1)$$

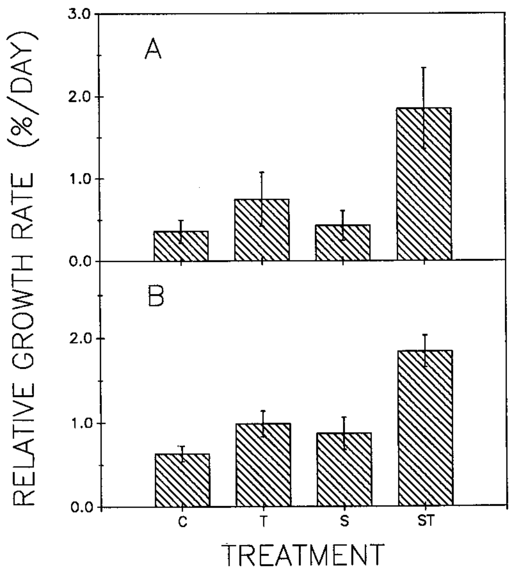

Fig. 2. Relative growth rates of above-ground dry weight of (A) *A. rubrum* seedlings planted in clumps of *R. glabra* ($N=6$) and (B) *F. americana* seedlings planted in clumps of *C. racemosa* ($N=8$). Both experiments were conducted in the Saccomanda old field. See the legend of Fig. 1 for an explanation of the treatments.

where S was the size at either Time 1 (27 June) or Time 2 (28 August).

Treatment effects were assessed for each field and each species combination separately by analysis of variance with shrub clumps as blocks and treatments randomized within clumps in a 2×2 factorial design (Statistical Analysis Systems, 1987); we also tested for site$\times$treatment interactions for *A. rubrum* seedlings planted in *C. racemosa* clumps with analysis of variance.

RESULTS

Guy-wiring shrub stems increased canopy openness over planted tree seedlings from 4–5% before treatment to 76–91% after treatment (Tables 1 and 2). When the guy ropes were removed at the end of the experiment, the shrub stems that were tied back supported what appeared to be complete canopies of leaves. This suggests that water and nutrients use by the guyed shrubs were not greatly reduced by the treatments; evaporation from the soil surface, however, probably did increase in response to canopy opening. Roots did not penetrate the root restriction cloth barriers during the experiment.

Relative growth rates for basal area, height, and above-ground biomass are presented (Tables 1 and 2) but we focus on the results for relative growth rates in biomass (Figs. 1 and 2). There were significant treatment effects on relative growth rates in basal area, height, and above-ground biomass of *A.*

rubrum seedlings planted in *C. racemosa* clumps within all three fields ($P<0.01$ for all F values). There were also significant interactions between the sun treatment and site ($F=6.9$, $P<0.05$) and trenching and site ($F=3.2$, $P<0.05$). Within-field contrasts revealed that for *A. rubrum* seedlings planted in *C. racemosa* clumps in the wettest field (lowland), above-ground biomass accumulation rates were highest for seedlings over which the shrub canopy was experimentally opened but showed no indication of an independent trenching effect (Table 1). In contrast, seedlings in the driest field (Gifford) responded most to trenching, especially when combined with canopy opening. Relative growth rates of tree seedlings in the Saccomanda old field for all three combinations of shrub and tree species were significantly increased by both the sun and the trench treatments. For *A. rubrum* in *R. glabra* clumps and *F. americana* in *C. racemosa* clumps there were marginally significant ($P<0.1$) interactions between the treatments.

DISCUSSION

Whether tree growth in shrub-dominated old fields in New York is slowed more by root or shoot competition depends to a large extent on the species under consideration and site conditions. On wet and nutrient-rich sites, the competitive effects of shrubs on tree seedlings are apparently much more severe above ground than below ground. Trenching around tree seedlings planted in shrub clumps in our lowland site only had an effect on seedling growth above ground if combined with canopy opening. In old fields with drier and more nutrient-poor soils, in contrast, canopy opening only increased seedling growth when root competition was prevented. Changes in below-ground growth in response to the treatments were not determined due to difficulties in extracting entire root systems in the field.

The responses of *A. rubrum* seedlings to release from above-ground and below-ground competition from *C. racemosa* were repeated at the intermediate site (Saccomanda) with *F. americana* planted under *C. racemosa* and *A. rubrum* planted under *R. glabra*. Judging from the relative effects of *R. glabra* and *C. racemosa* on above-ground growth of *A. rubrum, C. racemosa* seems to be a more potent competitor both above ground and below ground. *Fraxinus americana* seedlings in *C. racemosa* clumps grew more rapidly in the control treatments and responded less dramatically than *A. rubrum* to both trenching and canopy opening; these results suggest that *F. americana* seedlings suffer competition from *C. racemosa* but to a lesser extent than *A. rubrum* seedlings.

The controversy over whether plant competition is more intense below ground or above ground has flared up repeatedly but was most heated earlier in this century (e.g. Pearson, 1929; Toumey, 1929; Shirley, 1943). Advocates of the importance of root competition felt, and to some extent still feel, slighted insofar as although there is ample evidence that below-ground interactions are often very important, many studies on regeneration processes are still focused solely on light effects. Gaps in forests created by the death of large trees, for example, are still often treated as if the only effects are above ground (but see Vitousek and Denslow, 1986; Becker et al., 1988; Sanford, 1989). Our results suggest that polarization of opinion in this debate was unnecessary insofar as the location of the most intense competition depends on site conditions. Relative size of the interacting species is also important: once trees grow to be taller than shrubs, the root versus shoot competition debate becomes moot.

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